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XIPHIORHYNCHUS KIMBLALOCKI, A NEW BILLFISH FROM THE EOCENE OF MISSISSIPPI WITH REMARKS ON THE SYSTEMATICS OF XIPHIROID FISHES

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ABSTRACT: *Xiphiorhynchus kimblalocki*, a new species of extinct billfish from the Eocene of Mississippi, is described. This is the first record of *Xiphiorhynchus* outside of western Europe, and the material consists of a well-preserved rostrum, three partial vertebrae and two fin spine fragments. *Xiphiorhynchus kimblalocki* is compared with other living and extinct billfish and appears to be intermediate in morphology between the Xiphiidae and Istiophoridae. Various genera of fossil billfish are critically discussed and we suggest that the Blochiidae, Paleorhynchidae, and the "*Cylindracanthus*-group" should be placed in Xiphioidae *Incertae sedis* until better evidence indicates that they are billfish. We speculate that *Xiphiorhynchus* is an extinct offshoot from an unknown pre-Eocene common ancestor between Xiphiidae and Istiophoridae and is closer to the Istiophoridae than to the Xiphiidae. We also agree with earlier workers that the lineages of the Xiphiidae and Istiophoridae run back separately into basal Eocene times and that any common ancestry to each other and to the scombroids must have been prior to the Eocene and may have extended into the Cretaceous.

Billfish remains have been described in rocks from the Cretaceous Age (Dixon, 1850) to the Pleistocene (Fierstine and Appligate, 1968). The exact taxon to which many of these remains belong has puzzled paleontologists because identifications are usually based on isolated skeletal parts, particularly the rostrum. Detailed anatomical comparisons of recent genera are lacking and the lack of information has led to nomenclatorial confusion and misidentification of the fossil forms. Various attempts have been made to synthesize the avail-

able evidence and to make order out of chaos (Woodward, 1901; Leriche, 1905; Carter, 1927; Casier, 1946, 1966). Unfortunately, even the

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latest monograph (Casier, 1966) has failed to apply the well-established nomenclature and biological knowledge used by recent ichthyologists (Greenwood, Rosen, Weitzman, and Myers, 1966; Gosline, 1968; Howard and Ueyanagi, 1965; Morrow and Harbo, 1969; Nakamura, Iwai, and Matsubara, 1968; Robins and de Sylva, 1960, 1963). Thus, it is the object of this paper to describe a new species from the Eocene of Mississippi and to put at least a part of the fossil billfish problem in a more modern perspective.

SYSTEMATIC DESCRIPTION

CLASS OSTEICHTHYES

Order Perciformes

Suborder Xiphioidae

Family Xiphiorhynchidae

Genus *Xiphiorhynchus*, Van Benden, 1871

Xiphiorhynchus kimblalocki, new species Figures 1-4

Holotype: LACM 25575.1, a rostrum (Figs. 1, 2); LACM 25575.2, a partial anterior abdominal vertebra (Fig. 3); LACM 25575.3, a partial posterior caudal vertebra (Fig. 3); LACM 25575.4, a vertebral frag-

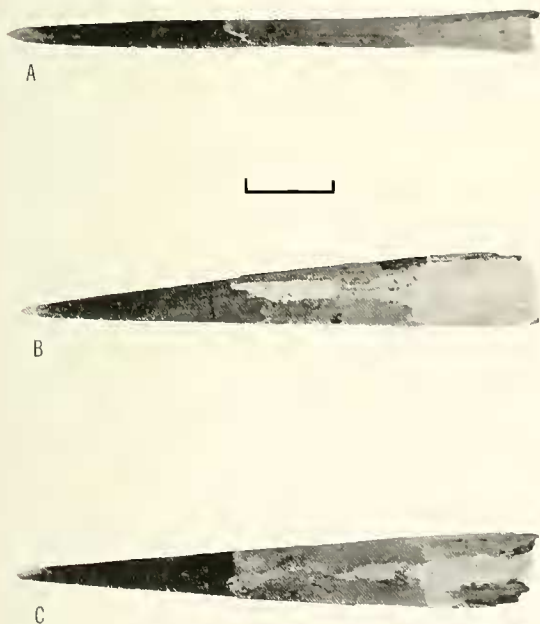


Figure 1. Rostrum of *Xiphiorhynchus kimblalocki*, new species (Holotype—LACM 25575.1): A. lateral view; B. ventral view; C. dorsal view. Scale equals 10 cm.

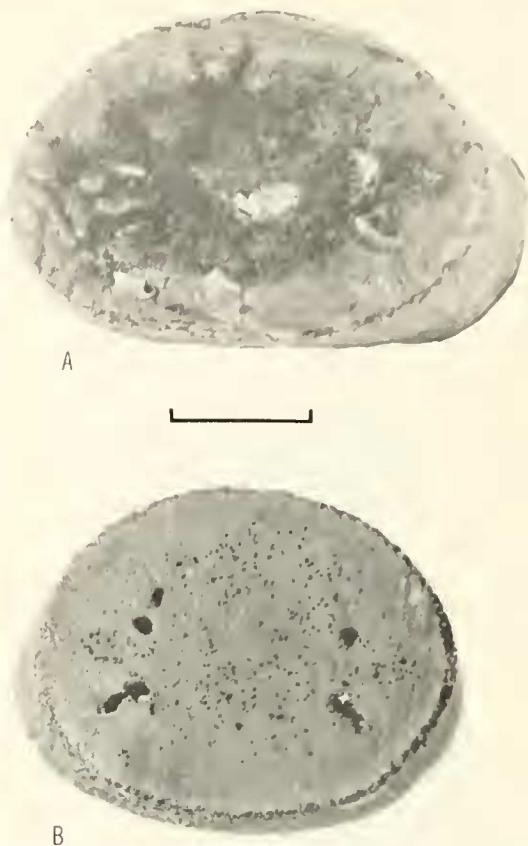


Figure 2. Rostrum of *Xiphiorhynchus kimblalocki*, new species (Holotype—LACM 25575.1): A. cross-section 220 mm from distal tip; B. cross-section 170 mm from distal tip. Scale equals 15 mm.

ment: LACM 25575.5, a partial fin spine (Fig. 4); LACM 25575.6, a partial fin spine (unfigured).

Horizon and Locality: LACM locality 7003, Scott Co., Mississippi, Southwest side of Sherman Hill (Hill 618), NW $\frac{1}{4}$ SW $\frac{1}{4}$ Sec 16, T5N, R9E, Forest (?Hill) Quadrangle, U.S.G.S., 1950. The specimens were collected in the Shubuta Clay member of the Yazoo Formation, Jackson Group (Eocene). The Shubuta consists of green to greenish-gray calcareous to non-calcareous, glauconitic, fossiliferous, silty clays (DeVries, *et al.*, 1963). Selenite crystals are common. There is no indication that the fossil was collected near the base or near the top of the formation. The associated fauna consisted of a skull and cervical vertebrae of *Zygorhiza kochi*, an extinct, primitive cetacean.

The species is named in honor of Mr. Kim Blalock who collected the specimens and discovered the site.

Diagnosis: The rostrum differs from other *Xiphiorhynchus* in its large size, rugose surface texture, lack of a central longitudinal nutrient canal at its distal end, and its diminutive alveoli.

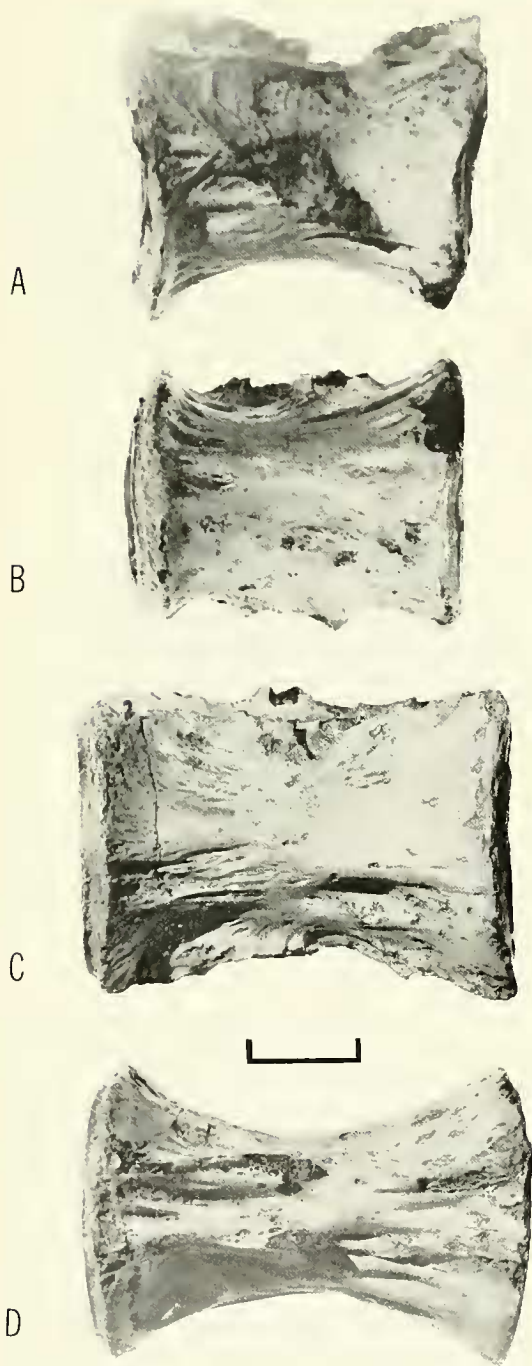


Figure 3. Vertebrae of *Xiphiorhynchus kimblalocki*, new species (Holotype): A. partial abdominal vertebra (LACM 25575.2), lateral view; B. partial abdominal vertebra (LACM 25575.2), ventral view; C. partial caudal vertebra (LACM 25575.3), lateral view; D. partial caudal vertebra (LACM 25575.3), ventral view. Scale equals 25 mm.

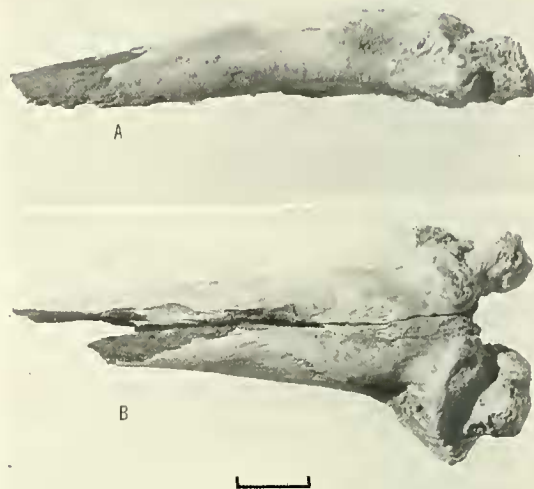


Figure 4. Fin spine of *Xiphiorhynchus kimblalocki*, new species (Holotype—LACM 25575.5): A. lateral view; B. anterior view. Scale equals 10 mm.

Description: The greatest length of the rostrum is 580 mm; it is nearly circular in cross-section at its distal tip and it becomes progressively larger and more depressed in cross-section towards its proximal end. One centimeter from the distal tip, the rostrum measures 11 mm wide and 12 mm thick, and the proximal end (base) is 83.5 mm wide and 38.0 mm thick. The proximal one-half probably was slightly depressed and crushed during preservation.

The dorsal surface is rugose at its distal end and longitudinally striated at its proximal end. Ventrally, the distal one-half is rugose. A poorly preserved alveolar layer covers the middle one-half of the ventral surface of the rostrum. The alveoli range from .25 to .4 mm in diameter. The proximal one-fourth of the ventral surface is not preserved.

A cross-section of the rostrum (Fig. 2), cut 220 mm from the distal tip, revealed poorly preserved bone. Traces of matrix revealed a central longitudinal nutrient canal which is bordered laterally by a pair of smaller lateral longitudinal nutrient canals.

A cross-section of the rostrum 170 mm from the distal tip (Fig. 2) revealed three right lateral longitudinal nutrient canals and two left lateral longitudinal nutrient canals. The central longitudinal nutrient canal had terminated prior to this section.

The centrum (Fig. 3) of the anterior abdominal vertebra (LACM 25575.2) is 70 mm long and the anterior and posterior surfaces are nearly circular.

The ratio of the height (60.4 mm) of the centrum, measured at its anterior surface, to its greatest length (70.0 mm) is 0.86. The surface texture is rugose and contains many pits and fossae. In lateral view, the ventral surface is gently concave; in ventral view the lateral surfaces are relatively flat and do not have a "pinched-in" appearance. The neural arch is broken at its base, but appears to be divided into a larger anterior zygapophysis and a smaller posterior zygapophysis. A large rib attachment area is present on each lateral side.

The centrum (Fig. 3) of the posterior caudal vertebra (LACM 25575.3) is 92.5 mm long and the anterior and posterior surfaces are nearly circular. The ratio of the height (64 mm) of the centrum, measured at its posterior surface, to its greatest length (92.5 mm) is 0.69. The surface texture is rugose and contains many pits and fossae. In lateral view, the ventral surface is gently concave; in ventral view, the lateral surfaces are concave and present an hourglass outline. The zygapophyses and the neural and haemal arches are broken off at their bases.

The two partial fin spines (LACM 25575.5 and LACM 25575.6) belong to a median (anal or dorsal) fin (Fig. 4). LACM 25575.5 measures 34 mm across its nearly complete base and 72 mm long. Although its distal tip is missing, it appears to have tapered rapidly to a point. When viewed from the side, it shows a slight posterior curvature. If the spine had been complete, we estimate that it would have measured 112 mm long and 40 mm wide. LACM 25575.6 is a left or right half of a spine that measures 20 mm across its base and 138 mm in length. When viewed from the side, it shows no antero-posterior curvature. If the spine had been complete, we estimate it would have measured 40 mm across its base and 210 mm in length.

DISCUSSION

The rostrum of *Xiphiorhynchus kimblalocki*, like other species of *Xiphiorhynchus* (Leriche, 1905; Casier, 1966), is similar in morphology to those found in the Istiophoridae (Tables 1 and 2). It differs, however, in the number of nutrient canals (Table 2), in having smaller alveoli, and in having a more depressed cross-section at its base (Table 1). The longitudinal openings, revealed in transverse section (Fig. 2), can be called nutrient canals with some assurance, since histological examination of the rostrum of a striped marlin (*Tetrapturus audax*) revealed blood vessels within the canals (Vladimir Walters, Univ. California, Los Angeles, unpublished).

The rostrum of the swordfish (*Xiphias gladius*), when compared to the rostrum of *X. kimblalocki*,

is more greatly depressed along its entire length. However, measurements taken at the base of the rostrum (Table 1) show that *X. kimblalocki* and *X. gladius* are nearly equally depressed. As noted earlier, some of the depression at the base of the rostrum in *X. kimblalocki* may be due to deformation during preservation. The rostrum of the swordfish lacks alveoli and denticles, but it does contain a central (? nutrient) canal and one pair of lateral nutrient canals.

The rostra of *Blochini* and what we are calling the *Cylindracanthus*-group (*Aglyptorhynchus*, *Congorhynchus*, *Cylindracanthus*, *Glyptorhynchus*, *Hemirhabdorrhynchus*, etc.) are much smaller than the rostra considered above. They all probably have numerous longitudinal nutrient canals (Carter, 1927; Casier, 1966; Fierstine and Applegate, unpublished).

The two vertebrae of *X. kimblalocki* differ from those of other billfish (Table 3). The anterior abdominal vertebra is similar in size and shape to a third or fourth abdominal of a black marlin (*Makaira indica*). It differs, however, in its rugose surface texture (the centrum of the black marlin is relatively smooth), the lack of a fossa on its ventral surface, and the shape and placement of its rib attachment. The third vertebra of the black marlin lacks a pronounced transverse process and has a large oval scar for rib attachment. The transverse process of *X. kimblalocki* is broken at its base, but it probably was large and quite pronounced.

The third vertebra of *X. gladius* has a thin, well-developed transverse process and no obvious rib facet. In this respect, the centrum of *X. gladius* is similar to the centrum of *X. kimblalocki*. The third vertebra of the swordfish (like most other vertebrae in the vertebral column) is more lightly constructed, appears to be more weakly ossified, and the surface architecture is smoother than for the abdominal vertebra of *X. kimblalocki*.

The caudal vertebra of *X. kimblalocki* differs considerably from any istiophorid caudal vertebra. It most closely resembles one from the posterior caudal region (approximately in the vicinity of the 21st vertebra). The height to length ratio of the centrum is much larger than the ratio for the three living istiophorid genera (Table 3). Thus, the caudal vertebra of *X. kimblalocki* is much more cube-like than those found in the Istiophoridae. The height to length ratio of the centrum compares much more favorably with the 21st centrum of *X. gladius*. The probable placement of the neural and haemal spines is similar.

TABLE 1. Height to width ratios of the rostra of certain billfish.

Species	Base	Middle Point	Tip (-1 cm)
<i>Istiophorus platypterus</i> (Sailfish)	$\frac{18}{22} = .82$	$\frac{13.5}{17.5} = .80$	$\frac{8}{11} = .73$
<i>Makaira indica</i> (Black marlin)	$\frac{46.5}{66.0} = .70$	$\frac{36.0}{43.5} = .83$	Missing
<i>Tetrapturus audax</i> (Striped marlin)	$\frac{22}{37.5} = .59$	$\frac{15.0}{22.5} = .67$	$\frac{5.2}{7.2} = .72$
<i>Xiphias gladius</i> (Swordfish)	$\frac{39}{89} = .44$	$\frac{18}{60} = .30$	$\frac{11}{39} = .28$
<i>Xiphiorhynchus kimblalocki</i>	$\frac{38}{83.5} = .46$	$\frac{35.3}{57.0} = .62$	$\frac{11}{12} = .92$

but as with the anterior caudal vertebra, the surface texture and construction is much more rugose and massive in *X. kimblalocki* than in the swordfish.

Casier (1966) described and figured from the London Clay, a vertebra that he identified as *Xiphiorhynchus* (?). This centrum is very similar in shape and preservation to the caudal vertebra of *X. kimblalocki*.

Systematics of the Xiphioid Fishes.—Fierstine and Walters (1968) and Gosline (1968) independently concluded that the Istiophoridae and Xiphiidae should be placed in the perciform suborder Xiphiioidei apart from the Scombroidei. Both followed Regan's (1909) and Gregory and Conrad's (1937) view that the Xiphiidae and Istiophoridae extend into basal Eocene time and that any common ancestry to each other and to the scombroids must have been prior to the Eocene and may have extended to the Cretaceous. These phylogenetic conclusions were partially based on the identifications by paleontologists who we now believe were in error. The following discussion is a critical review of billfish phylogeny and classification based primarily on fossil forms.

Woodward (1901) recognized that the Xiphiidae included all living billfish genera, as well as *Xiphiorhynchus*, *Acestrus*, and *Brachyrhynchus*. All the xiphiids were placed in the Division Scombriformes along with the scombrids, carangids, stromateids, and the extinct family Palaeorhynchidae. Woodward placed *Blochi* in the family Blochiidae in the division Blenniiformes. Regan (1909) placed the billfish in their own division, Xiphiiformes, within the perciform suborder Scombroidei. In this division he separated the istiophorids, xiphiids, and xiphiorhynchids into

their own families. In addition, Regan included the blochiids as a family within the Xiphiiformes.

The placement of the Paleorhynchidae with the xiphioids has been labeled as dubious (Gosline, 1968). According to Danil'chenko (1960), the paleorhynchids have about 45–60 vertebrae, jaws which are very clongate with the lower jaw sometimes longer than the upper, and ribs which completely surround the abdominal cavity. Thus, the paleorhynchids have about twice the vertebral number and have jaws and ribs unlike any living adult xiphioid. Until the paleorhynchids have been thoroughly studied, we prefer to put them in the Xiphiioidei *Incertae sedis*.

Woodward (1942) stated that *Blochi* does not exhibit the character of a xiphioid. Specimens of *Blochi* have a low vertebral number (24) and they lack (or have very reduced) pelvic fins, a condition similar to that found in living swordfish. However, blochiids are small (about 1 meter), have numerous dorsal and anal spines, have large scales, a round bill, and were living contemporaneously with the various species of *Xiphiorhynchus* and some istiophorids. Without question, the blochiids need additional study in order to determine their relationship and, until such research is accomplished, we prefer to put the Blochiidae in the Xiphiioidei *Incertae sedis*.

The relationship of the *Cylindracanthus*-group to the Xiphiioidei is also highly questionable. This group is only known by fossil rostra; no other skeletal remains have ever been positively identified. Encouraged by Woodward, Carter (1927) studied a *Cylindracanthus* rostrum from the Eocene of Nigeria. He showed that it was histologically similar to a fragment of a *Blochi* rostrum as well as to a dermal spine of an un-

TABLE 2. Rostral characters and chronological and geographical distributions of various billfish genera

Comparative Rostral Characters			
Taxon	Size and Shape of Cross-Section	Number of Longitudinal Nutrient Canals	Chronologic and Geographic Range
BLOCHIIDAE			
+ <i>Blochius</i>	small, round	unknown	Eocene, Europe
+ <i>Cylindracanthus</i> group	small, round	numerous	Cretaceous, Africa, Europe, North America to Oligocene, Europe
ISTIOPHORIDAE			
+ <i>Acestrus</i>	unknown	unknown	Eocene, Europe
<i>Istiophorus</i>	large, round	one pair	Eocene, Europe, N
<i>Makaira</i>	large, round	one pair	America to recent,
<i>Tetrapturus</i>	large, round	one pair	world-wide seas.
+ <i>Brachyrhynchus</i>	large, round	one pair	Eocene to Pliocene, Europe
PALEORHYNCHIDAE			
+ <i>Enniskillenius</i>	unknown	unknown	Eocene, Europe
+ <i>Homorhynchus</i>	unknown	unknown	Eocene to Oligocene, Europe
+ <i>Paleorhynchus</i>	unknown	unknown	
+ <i>Pseudotetrapturus</i>	(?) large, round	unknown	
XIPHIIDAE			
<i>Xiphias</i>	large, depressed	central and one pair	Oligocene, Europe to recent, world-wide seas.
+ undescribed genus	large, depressed	(?) central and one pair	Eocene, North America
XIPHIORHYNCHIDAE			
+ <i>Xiphiorhynchus</i>	large, round	central and two pair	Eocene, Europe, N. America, Africa

+ = extinct

related living trunkfish (*Ostracion*). He concluded that the *Cylindracanthus* specimen was probably the bill of some extinct swordfish related to *Blochius*. This relationship has been accepted by most other ichthyologists and paleontologists (Berg, 1940; Casier, 1946, 1958; Darteville and Casier, 1943, 1949; Gregory, 1951; Leriche, 1942; and Romer, 1966). Recently Casier (1966) divided the *Cylindracanthus*-group into two parts and questionably put one part in the family Blochiidae of the Order Heteromi and the remainder in family Xiphiidae of the Order Scombromorphi (= ?Scombroidei). No explanation was given as to why he thought there was a relationship to the Order Heteromi (= Notacanthiformes). Woodward (1942) placed *Cylindracanthus* (= *Coelorhynchus*) in *Incertae sedis* and we agree with this decision. The transfer of the *Cylindracanthus*-group from the Xiphiidae proper removes all the pre-Eocene representatives.

On the basis of the above discussion, the seven

genera: *Acestrus*, *Brachyrhynchus*, *Istiophorus*, *Makaira*, *Tetrapturus*, *Xiphias*, and *Xiphiorhynchus* are all that remain as members of the Xiphiidae proper. Beginning with the living genera, we can reiterate that the Xiphiidae (*Xiphias*) is structurally very different from the Istiophoridae (*Istiophorus*, *Makaira*, *Tetrapturus*). *Xiphias* has a poor fossil record. Leriche (1910) identified a vertebra from the Oligocene of Belgium as *Xiphias rupelensis*, and we agree with his identification since the specimen is very similar to the penultimate vertebra of *X. gladius*. As far as we know, all other fossil records are erroneously based on istiophorids or members of the *Cylindracanthus*-group. Except for the rostrum, the skeleton of *X. gladius* is rather weak and fragile so that preservation is probably poor.

Not enough osteological information is known to distinguish between the rostra, skulls or vertebrae of the various recent or fossil istiophorids; therefore, exact identifications of fossil forms.

TABLE 3. Height to length ratios of the centra of certain billfish.

Species	3rd Vertebra	21st Vertebra
<i>Istiophorus platypterus</i> (Sailfish)	$\frac{30.5}{57.0} = .54$	$\frac{24.0}{66.5} = .37$
<i>Makaira indica</i> (Black marlin)	$\frac{52.5}{62.5} = .84$	$\frac{38.5}{83.5} = .46$
<i>Tetrapturus audax</i> (Striped marlin)	$\frac{30}{47} = .64$	$\frac{24}{61} = .39$
<i>Xiphias gladius</i> (Swordfish)	$\frac{43.0}{62.5} = .69$	$\frac{54}{72} = .75$
	Abdominal Vertebra	Caudal Vertebra
<i>Xiphiorhynchus kimblalocki</i>	$\frac{60.4}{70.0} = .86$	$\frac{64.0}{92.5} = .69$

which are usually fragmentary, are to be questioned. Some of the fossil rostra may belong to *Xiphiorhynchus* and those identified as *Brachyrhynchus* are probably congeneric with *Istiophorus*, *Makaira*, or *Tetrapturus*. This latter observation was also noted by Woodward (1901). It seems, therefore, that *Brachyrhynchus* and the living istiophorids may form a continuum that dates from the Middle Eocene of Europe (Bruxellien).

Acestrus is only known from the early Eocene (London Clay-Ypresien) and the remains consist of posterior crania. Casier (1966) feels that these crania may belong to one of the other billfish genera, but not *Xiphiorhynchus*. *Acestrus*, like the living billfish, has pronounced muscle fossae on the dorsal surface of the posterior part of the cranium, whereas fossae seem to be lacking in *Xiphiorhynchus*. Casier (1966) also emphasizes that the cranium of *Acestrus* is very similar to that of the extinct scombroid, *Scombrinus*. All known cranial fragments of *Acestrus* are much smaller (they measure 50–60 mm in length) than the counterparts in living adult billfish and they are about one-half the size of the crania of *Xiphiorhynchus*. Even though the exact taxonomic placement of *Acestrus* is uncertain at best, we prefer to keep the genus in the Xiphiidae proper until more is known. It is possible that *Acestrus* is an immature billfish.

Xiphiorhynchus is intermediate in many respects to the Xiphiidae and Istiophoridae. Each frontal bone has ridges that radiate from a central point similar to the swordfish, whereas only the anterior

ridges are pronounced in the Istiophoridae. The ratio of the length of the posterior part of the cranium (anterior edge of the supraoccipital to the posterior edge of the exoccipital) to the length of the anterior part of the cranium (anterior edge of the mesethmoid to the posterior edge of the frontal) is about 0.35 for *Xiphiorhynchus priscus*, *T. audax*, *T. angustirostris*, *Istiophorus* sp. and *M. indica*. A similar ratio for *X. gladius* is 0.13, thus, the swordfish has a much smaller posterior region of the skull than other billfish.

The rostrum of *X. kimblalocki* appears to be broad at the base, similar to the swordfish, and it is round in the distal one-half, similar to the istiophorids (Table 1). Both the swordfish and *Xiphiorhynchus* have a central canal in their rostra, whereas the istiophorids have only lateral canals. However, *X. kimblalocki* lacks a central canal in the distal one-fourth of its rostrum. The abdominal vertebra of *X. kimblalocki* (Table 3) is similar in shape to the third vertebra of the black marlin (*M. indica*), yet the placement of the transverse process is similar to the third vertebra of the swordfish. In shape, the caudal vertebra of *X. kimblalocki* is similar to those of the swordfish.

It seems, therefore, that *Xiphiorhynchus* is intermediate between the Istiophoridae and the Xiphiidae and gives evidence that the two living billfish families diverged from a common ancestor prior to the Eocene. However, chronologically, *Xiphiorhynchus* is not able to be the common ancestor since it has never been found prior to the Eocene. There is no evidence that it is a

surviving parental stock. Very recently one of us (S.P.A.) collected a 75 cm section of a swordfish-like rostrum from the Yazoo Clay of the Eocene of Mississippi (Fierstine and Applegate, unpublished). This very depressed rostrum differs considerably from any rostrum known in Xiphiorhynchidae and Istiophoridae and demonstrates that a swordfish-like animal was living contemporaneously during the Eocene with the Xiphiorhynchidae and Istiophoridae. At this time we speculate that *Xiphiorhynchus* is an extinct offshoot from a yet unknown common ancestor and is closer to the Istiophoridae than to the Xiphiidae. Thus, even though based on different evidence, we must return to the conclusions of Regan (1909) and Gregory and Conrad (1937) that both the Xiphiidae and Istiophoridae extend into the basal Eocene and that any common ancestry to each other and to the scombroids must have been prior to the Eocene and may have extended to the Cretaceous.

Our proposed classification scheme for the billfish is as follows:

Class Osteichthyes

Order Perciformes

Suborder Xiphioidi

Family Istiophoridae: *Acestrus*, *Brachyrhynchus*, *Istiophorus*, *Makaira*, *Tetrapturus*.

Family Xiphiidae: *Xiphias* and undescribed genus.

Family Xiphiorhynchidae: *Xiphiorhynchus*.

Xiphioidi Incertae sedis.

Family Blochiidae: *Blochius*.

Family Paleorhynchidae: *Enniskillenius*, *Homorhynchus*, *Paleorhynchus*, *Pseudotetrapturus*.

Family unknown: *Cylindracanthus*-group.

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